

RESEARCH ARTICLE

Distinct community assembly processes underlie significant spatiotemporal dynamics of abundant and rare bacterioplankton in the Yangtze River

Malan Yi¹, Yao Fang¹, Guoping Hu², Shufeng Liu¹, Jinren Ni¹, Tang Liu (✉)^{3,4}

¹ College of Environmental Sciences and Engineering, Peking University, Key Laboratory of Water and Sediment Sciences (Ministry of Education), Beijing 100871, China

² Fluid Science and Resources Division, Department of Chemical Engineering, The University of Western Australia, Crawley, WA 6009, Australia

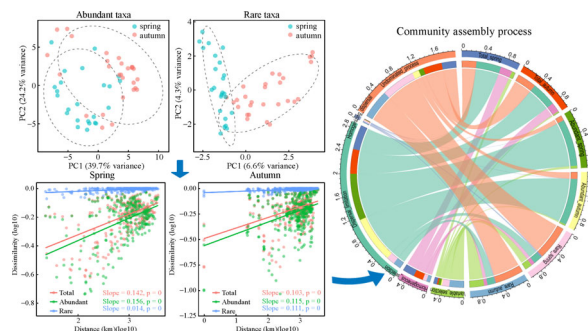
³ College of Chemistry and Environmental Engineering, Shenzhen University, Shenzhen 518060, China

⁴ State Environmental Protection Key Laboratory of All Material Fluxes in River Ecosystems, Peking University, Beijing 100871, China

HIGHLIGHTS

- Season and landform influenced spatiotemporal patterns of abundant and rare taxa.
- Different stochastic processes dominated abundant and rare subcommunity assembly.
- River flow and suspended solids regulated assembly processes of rare taxa.

GRAPHIC ABSTRACT



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ABSTRACT

The rare microbial biosphere provides broad ecological services and resilience to various ecosystems. Nevertheless, the biogeographical patterns and assembly processes of rare bacterioplankton communities in large rivers remain uncertain. In this study, we investigated the biogeography and community assembly processes of abundant and rare bacterioplankton taxa in the Yangtze River (China) covering a distance of 4300 km. The results revealed similar spatiotemporal patterns of abundant taxa (AT) and rare taxa (RT) at both taxonomic and phylogenetic levels, and analysis of similarities revealed that RT was significantly influenced by season and landform than AT. Furthermore, RT correlated with more environmental factors than AT, whereas environmental and spatial factors explained a lower proportion of community shifts in RT than in AT. The steeper distance-decay slopes in AT indicated higher spatial turnover rates of abundant subcommunities than rare subcommunities. The null model revealed that both AT and RT were mainly governed by stochastic processes. However, dispersal limitation primarily governed the AT, whereas the undominated process accounted for a higher fraction of stochastic processes in RT. River flow and suspended solids mediated the balance between the stochastic and deterministic processes in RT. The spatiotemporal dynamics and assembly processes of total taxa were more similar as AT than RT. This study provides new insights into both significant spatiotemporal dynamics and inconsistent assembly processes of AT and RT in large rivers.

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1 Introduction

Microorganisms are the unseen majority of organisms that sustain major biogeochemical cycles of macronutrients,

micronutrients and other elements, which are vital to other lives and ecosystem services (Falkowski et al., 2008; Guidi et al., 2016; Jansson and Hofmockel, 2020; Liu et al., 2021). However, understanding the biogeography and underlying assembly mechanisms of microbial communities presents a great challenge due to the complexity of ecological networks (Ma et al., 2016). Since the discovery

✉ Corresponding author
E-mail: liutang@pku.edu.cn

of tremendous microbial diversity at low relative abundance in marine water and sediment using high-throughput sequencing (Sogin et al., 2006), a skewed abundance distribution of microorganisms has been observed in various ecosystems (Jia et al., 2018; Jiao and Lu, 2020a). Microorganisms consist of a relatively small number of dominant species and several low-abundance species (Jia et al., 2018). These low-abundant organisms, namely “rare biosphere”, often comprise the majority of species in a local community, caused by the evolution of unicellular organisms over billions of years (Lynch and Neufeld, 2015). Although abundant microbial taxa are responsible for the majority of ecological functions (Cottrell and David, 2003; Pedrós-Alió, 2012), rare microbial taxa can also provide broad ecological services and resiliency (redundancy and flexibility) (Caron and Countway, 2009; Lynch and Neufeld, 2015). Previous studies have indicated that rare taxa (RT) often had a different distribution pattern compared to the abundant taxa (AT) (Pedrós-Alió, 2012; Wu et al., 2017). Therefore, further exploration of the differences in microbial biogeography and assembly processes between AT and RT will promote our understanding of ecosystem services and functions.

Most available studies investigating the biogeography of abundant and rare bacterial taxa have focused on soil, oceans and lakes (Wu et al., 2017; Peter et al., 2018; Ji et al., 2020; Jiao and Lu, 2020b; Wan et al., 2021b). However, large-scale knowledge on the spatiotemporal distribution of abundant and rare bacterial communities in rivers is still relatively limited (Wang et al., 2020). Bacteria contribute significantly to the metabolic functions and nutrient cycling in river ecosystems by coupling biogeochemical cycles between continents, lakes and their marine counterparts (Aufdenkampe et al., 2011). The spatiotemporal distribution of the microbial community in river ecosystems is rather diverse and dynamic and is often influenced by a combination of complex natural factors (e.g., temperature, nutrients, pH) (Staley et al., 2015; Sun et al., 2018; Liu et al., 2020; Zhang et al., 2020). Certain anthropogenic impacts (e.g., dam, sewage disposal, soil erosion) on the microplankton community have also been revealed across different scales (Liu et al., 2018). The abundant and rare microeukaryotic communities showed similar biogeographical patterns in a subtropical river (Chen et al., 2019). However, the differences between bacteria and microeukaryotes involving size, physiology and morphology may cause various responses to environmental changes.

Understanding the assembly process that influences biodiversity patterns is a popular topic in microbial ecology (Ning et al., 2019). Vellend’s conceptual framework describes the ecological processes embedded in dispersal, selection, speciation and drift (Vellend, 2010). Dispersal refers to the movement of individuals across space with successful relocation (Hanson et al., 2012). Selection results from a combination of environmental

factors (e.g., pH, salt and temperature) and interspecies interactions (e.g., predation, mutualism and competition) that alter community structure, which varies with the habitat fitness of various species (Stegen et al., 2013; Zhou and Ning, 2017). Ecological drift is the result of the fluctuation of population sizes caused by chance events, such as birth, death, and reproduction, which are inherent random processes of organisms (Vellend, 2010). Speciation denotes the generation of new species by an evolutionary process that enhances species diversity (Vellend, 2010; Nemergut et al., 2013). Among these procedures, selection is the central to niche-based theory, while dispersal, drift, and speciation are stochastic processes (Vellend, 2010). Wu et al. (2017) revealed that dispersion had a larger influence on abundant subcommunities than on rare subcommunities in the north-western Pacific Ocean. A similar pattern was observed in fungal communities in agricultural soils across eastern China (Jiao and Lu, 2020a). In contrast, rare bacterial subcommunities were found to be limited by dispersion than abundant bacterial subcommunities in three subtropical bays in China (Mo et al., 2018). For river ecosystems, prior studies have revealed that stochastic processes shaped microbial communities across different seasons and scales using the null model (Chen et al., 2019). However, quantifying bacterioplankton community assembly processes in river ecosystems, especially to distinguish between AT and RT, is far less appreciated.

Our previous study revealed biogeographic patterns of bacterial communities in the Yangtze River (China), the third longest river in the world (Liu et al., 2018). Here, based on the existing data sets of high-throughput 16S rRNA sequencing of the Yangtze River, we further characterized the distribution and assembly processes of abundant and rare bacterioplankton communities. The data ranging from Shigu, Yunnan Province (China) (4300 river kilometer, rkm) to the river mouth (Xuliujing, Jiangsu Province, China) were collected in spring and autumn in 2014, and were used for bioinformatics analysis. In this study, we aimed to 1) disclose the biogeographic patterns of abundant and rare planktonic bacterial communities in the Yangtze River; 2) quantify the underlying community assembly processes of abundant and rare bacterial taxa using the null model. Considering the minor influences of speciation within metacommunity (Leibold et al., 2004), only selection, dispersal and undominated process (consisting of weak selection, weak dispersal, diversification, and/or drift) were considered to control turnover in community composition.

2 Methods

2.1 Sequencing data sets

The high-throughput sequencing data of the bacterial 16S

rRNA gene was obtained from our previous research on bacterial diversity in the Yangtze River of China (Liu et al., 2018). Briefly, 48 water samples (10 L) were collected from 24 sampling sections across the mainstream of the Yangtze River in March (spring) and October (autumn), 2014. In addition, four parallel samples were taken from four sampling sections (Site 10, 11, 12 and 13) in autumn. These 24 sampling sites were located at five geographic regions: mountain region (Hengduan Mountains: site 1–2), hill region (South Sichuan Hill: site 3–5), basin region (Sichuan Basin: site 6–9), hill-mountain region (Three Gorges: site 10–13), and plain (middle – lower Yangtze Plain: 14–24). The locations of these 24 sampling sites could be seen in our previous study (Liu et al., 2018). These water samples were filtered using 0.22 µm pore-size polycarbonate membranes (Millipore, USA). Subsequently, the membranes were used for DNA extraction, PCR amplification of the V4–V5 region of the bacterial 16S rRNA gene, and Illumina sequencing.

Seventeen environmental factors were measured using standard water testing protocols (Sun et al., 2016) while sampling, which included pH, water temperature (T), water hardness (WH), electrical conductivity (EC), total nitrogen (TN), suspended solids (SS), river flow (Q), dissolved oxygen (DO), nitrate nitrogen (NO_3^-), ammonium nitrogen (NH_4^+), total phosphorus (TP), sulfate ion (SO_4^{2-}), chloride ion (Cl^-), dissolved organic carbon (DOC), fluoride ion (F^-), chemical oxygen demand (COD) and biological oxygen demand (BOD).

2.2 Bioinformatics

QIIME2 (Bolyen et al., 2019) was used for bioinformatics analysis of the 16S rRNA gene sequences. The paired-end reads were merged and quality-filtered using VSEARCH (Rognes et al., 2016) with default parameters. The Deblur plugin (Amir et al., 2017) was used for denoising and generating amplicon sequence variants (ASVs). ASVs with fewer than 10 sequences across all samples were discarded. Taxonomic classification of ASVs was performed with classify-sklearn (Bokulich et al., 2018) using the Silva 16S rRNA database (138, 99% clustered) (Quast et al., 2013) and ASVs annotated as mitochondria or chloroplasts were removed. A phylogenetic tree was constructed using the pipeline align-to-tree-mafft-fasttree (Price et al., 2010; Katoh and Standley, 2013). Thereafter, the sequence data were rarefied to 11080 sequences per sample for subsequent analysis. The abundant taxa (AT) are defined as ASVs with relative mean abundances higher than 0.1%, and the rare taxa (RT) as those lower than 0.01% (Jiao and Lu, 2020b; Nyirabuhoro et al., 2020).

2.3 Alpha and Beta diversity

Alpha diversity was assessed by taxonomic and phyloge-

netic metrics. The taxonomic metrics, including ASV richness, Chao extrapolative richness estimator, Pielou's evenness and Shannon index, were calculated using R-4.0.0 with vegan 2.5-6 package. The phylogenetic measures of diversity, such as Faith's phylogenetic diversity (PD), the PD divided by the number of ASVs (PD/ASVs) and the unweighted mean nearest taxon distance (MNTD), were computed using R-4.0.0 with vegan 2.5-6 and picante 1.8.2 package. The diversity indices amid seasonal variations were tested using the paired *t*-test if the data followed a normal distribution and had homoscedasticity of error variances, otherwise tested using the paired Wilcoxon signed-rank test.

Bray-Curtis, Sørensen, unweighted UniFrac and weighted UniFrac metrics were used to compute the pairwise dissimilarities among samples for total, abundant and rare (sub)communities, and to explore the beta diversity of bacterial assemblages. Principal coordinates analysis (PCoA) was employed for the visualization of the four distance matrices. The significance of seasonal variation was evaluated by analysis of similarities (ANOSIM) with the parameter strata as the sampling site. All analyses were performed using R-4.0.0, with the vegan 2.5-6 and PhyloMeasures 2.1 package.

2.4 The distance-decay patterns

The distance from each sampling site to the river mouth along the river was determined using ArcGIS V10.2 software. The slopes of a linear least squares regression based on log-transformed geographical distance and log-transformed Bray-Curtis and unweighted UniFrac distance matrices of bacterial communities were calculated as the rate of the distance-decay patterns. Permutational test (999 times) were used to test the fitting of distance-decay patterns to the classic power-law function. Significance tests were conducted to assess the difference in slopes by R-4.0.0 with simba 0.3-5 package.

2.5 Correlation of environmental factors and bacterial communities

The correlation between environmental factors, and Mantel tests between environmental factors and bacterial community structures based on Bray-Curtis and unweighted UniFrac were performed using R-4.0.0 with ggcor 0.9.8 package. Variance partitioning analysis (VPA) was conducted based on RDA to compare the effects of environmental and spatial factors on governing community structures by R-4.0.0 with vegan 2.5-6 package. As co-variation might occur among these environmental factors, forward selection based on adjusted R^2 was used for selecting explanatory variables while minimizing the influence of collinearity. Wherever possible, $p < 0.05$ (adjusted by false discovery rate) was considered significant.

2.6 Estimating influences of ecological processes

To quantify the effects of assembly processes in the bacterial communities, we calculated the β -nearest taxon index (β NTI) and Bray-Curtis-based Raup-Crick metric (RCbray) based on the entire-community null model (ENM) (Stegen et al., 2013, 2015; Tripathi et al., 2018). A β NTI value less than -2 indicates that the phylogenetic turnover was significantly less than expected (homogeneous selection), whereas the phylogenetic turnover was significantly more than expected (variable selection), when the β NTI value was greater than 2 . If the absolute value of β NTI ($|\beta$ NTI) was smaller than 2 , deterministic selection was not the main reason for the observed difference in the phylogenetic community composition. RCbray was a metric of turnover in ASV composition. When $|\beta$ NTI is smaller than 2 , RCbray value less than -0.95 indicates that the turnover in community composition was primarily determined by homogenizing dispersal; RCbray values larger than 0.95 , indicates that the turnover in community composition is primarily governed by dispersal limitation, and the absolute value of RCbray ($|\text{RCbray}|$) less than 0.95 , indicates that no single process dominates community assembly, consisting of weak selection, weak dispersal, diversification, and/or drift (undominated process). Furthermore, phylogenetic bin-based null model analysis (iCAMP) was also conducted using R-4.0.0 with iCAMP 1.3.4 package (Ning et al., 2020). In addition, Mantel and partial Mantel (conditioned on distance along river) tests were conducted to compare all possible pairwise comparisons of β NTI values with each major environmental variable.

3 Results

3.1 Physicochemical characteristics of the Yangtze River

As described in the Methods section, 17 physicochemical parameters were investigated in this survey. Paired *t*-test and Wilcoxon signed-rank test were used to analyze the differences between spring and autumn. The results (Fig. S1) showed that more than two-thirds of these environmental factors exhibited a significant difference between the two seasons. The mean values of SS, Q and T in autumn were higher than those in spring, while the mean values of F^- , EC, NH_4^+ , NO_3^- , WH, SO_4^{2-} , DO and TP in autumn were lower than those in spring. This was due to the shift in the wet (autumn) and dry (spring) seasons during the year. There were no significant differences in other physicochemical parameters across different seasons. The correlation analysis (Fig. 1) showed that 36 paired correlations were significant (fdr, false discovery rate, adjusted $p < 0.05$) (Benjamini and Hochberg, 1995) for spring, while 56 significant correlations were observed in

autumn. This implied that these environmental factors were more connected in autumn than in spring.

3.2 Alpha diversity of community between both seasons

During quality filtration and removal of chimeric sequences were performed, a total of 5825 ASVs were generated using Deblur to denoise sequence data of the 52 samples and used for alpha diversity analysis. The two metrics of taxonomic alpha-diversity used here differed significantly between spring and autumn (paired *t*-test and Wilcoxon signed-rank test), with samples in autumn being richer in ASVs than those in spring (Fig. S2). However, the Shannon diversity and Pielou's evenness indices did not display significant differences between the two seasons, implying similar diversity when counting in relative abundance and evenness between them. The paired Wilcoxon rank sum test also showed that PD was significantly different with a higher phylogenetic diversity in autumn than in spring, while the other three metrics of phylogenetic diversity had no significant seasonal variation.

The relative average abundances of all samples were used to define AT and RT. More than half of the ASVs were identified as RT (55.0%), while they accounted for only 1.1% of the average relative abundance (Fig. S3). In contrast, the proportion of ASVs in AT was rather low (mean = 2.6%), accounting for 78.7% of the average relative abundance. The richness and relative abundance of ASVs of RT in autumn were higher than those in spring, while no significant differences in richness were observed for AT between the two seasons.

3.3 Spatiotemporal distribution patterns of abundant and rare taxa

We studied stations spanning a longitudinal gradient of 4300 km along the Yangtze River from Shigu (Yunnan, China) to Xuliujing (Shanghai, China) for two seasons. The PCoA ordinations based on Bray-Curtis distance indicated that the bacterial community compositions (including total taxa, AT, and RT) differed significantly between spring and autumn (Fig. 2). The ANOSIM tests with $p < 0.001$, confirmed seasonal differences (Table S1). However, the seasonal variation in the total taxa ($R = 0.388$) was lower than that in RT ($R = 0.551$), and larger than that in AT ($R = 0.317$). The ANOSIM and PCoA ordinations based on Sørensen, unweighted UniFrac and weighted UniFrac distance also showed a similar dynamic (Figs. S4–S6 and Table S1). Mantel test was used for correlating the total community composition with abundant and rare subcommunity composition (Table S2). The results revealed that AT had higher *R* values than RT for all unweighted and weighted metrics (Sørensen, Bray-Curtis, unweighted UniFrac and weighted UniFrac distance). Venn

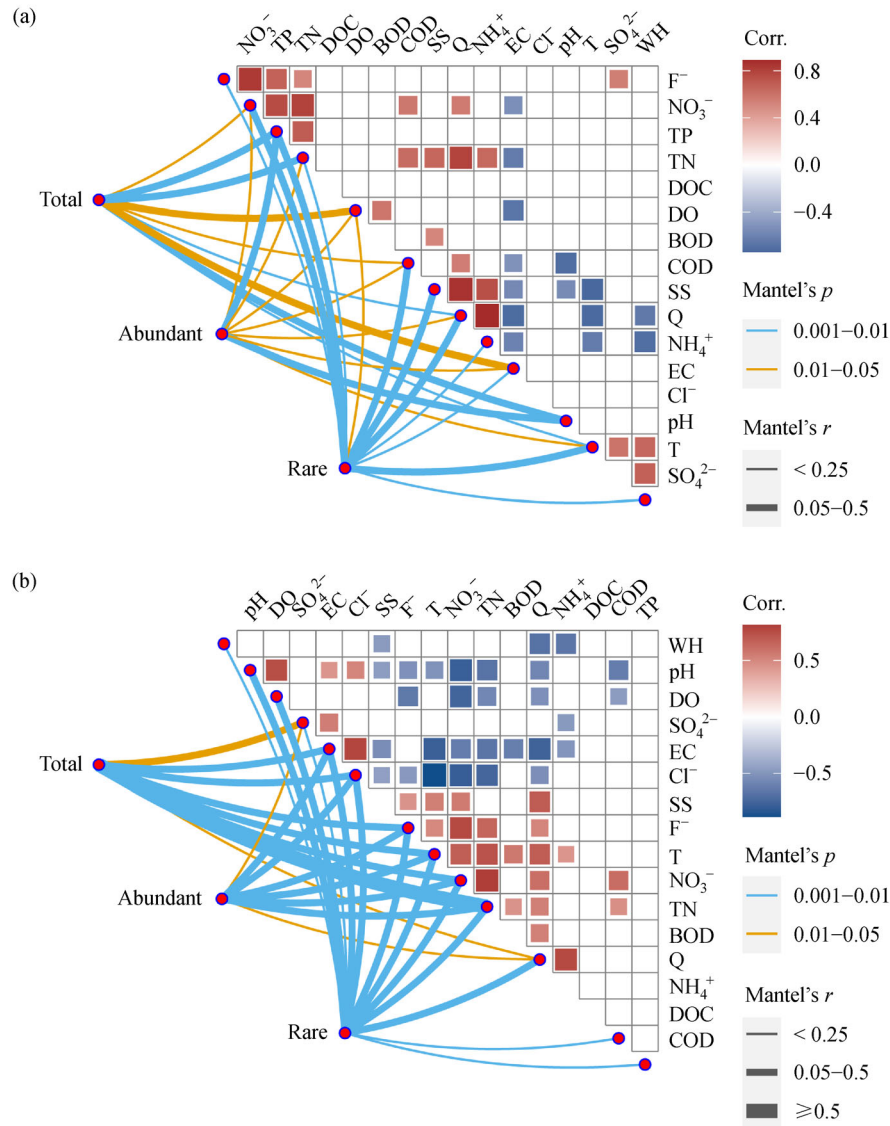


Fig. 1 Environmental drivers of the total, abundant and rare bacterioplankton communities for spring (a) and autumn (b). Pairwise Pearson's correlation coefficients among environmental factors with $p > 0.05$ are showed with a color gradient. Mantel tests are performed for relating bacterial community composition (Bray-Curtis distance) with environmental factors. The edge width denotes Mantel's r value, and edge color indicates the Mantel's p value based on 999 permutations. These abbreviations of environmental factors are the same as those in Methods and Fig. S1.

diagrams indicated that the proportion of ASVs shared between the two seasons varied among different communities (24.8% for total taxa, 77.8% for AT, and 9.0% for RT; Fig. S7). In conclusion, AT had larger community compositions variation and a smaller proportion of shared ASVs between spring and autumn than RT.

PCoA plots of each season were designed to further investigate the spatial patterns of the bacterial communities (Fig. 3). According to the landforms through which the river flows, all the samples were generally partitioned into five geographic clusters: mountain region, hill region, basin region, hill-mountain region and plain. The PCoA for each season showed clear spatial patterns of the bacterial

community compositions (including total taxa, AT and RT), and all the samples were partitioned into five geographic clusters corresponding to the types of landforms (Figs. 3 and S8). The Bray-Curtis dissimilarities were higher between groups rather than those within groups, except for the mountain group that had relatively higher dissimilarity within the group (Tables S3–S8). The results of ANOSIM (Table S9) revealed that most cluster-to-cluster variations were significant, further supporting this pattern. Most inapparent variations always occurred in mountain-included pairs, which resulted from large community structure difference within mountain group.

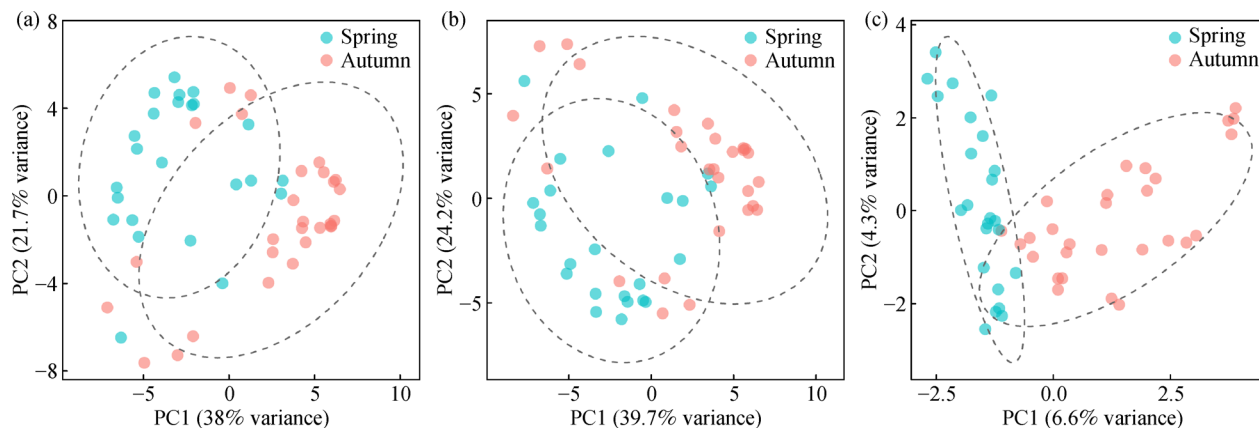


Fig. 2 Principal coordinates analysis of all samples for total (a), abundant (b) and rare (c) bacterial (sub)communities. The Bray-Curtis distance is used for quantifying the community compositional variation. Red indicates autumn, and blue indicates spring.

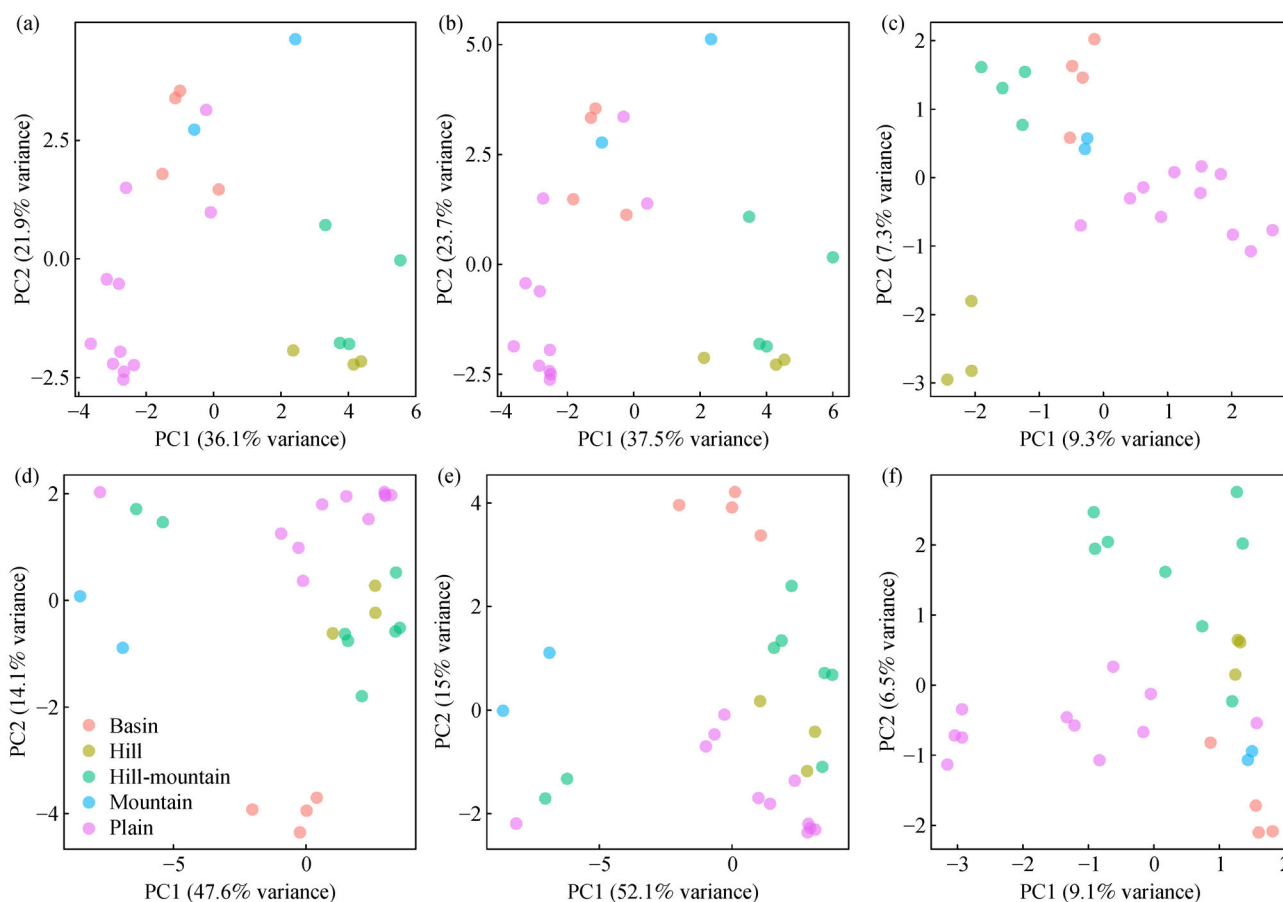


Fig. 3 Principal coordinates analysis showing the bacterioplankton community composition among different landforms in the total-spring (a), abundant-spring (b), rare-spring (c), total-autumn (d), abundant-autumn (e), and rare-autumn (f) samples. The Bray-Curtis distance is used for quantifying the community compositional variation.

3.4 Environmental and spatial responses of abundant and rare taxa

The correlations between community composition and

main environmental factors were used to evaluate the influences of environmental factors on community. For spring, Mantel test results indicated that nine factors (e.g., DO, EC, TN, T, and Q) were significantly associated with

abundant subcommunity (fdr adjusted $p < 0.05$; Fig. 1(a)), with the same nine factors having significant effects on the total community. Rare subcommunity covaried significantly with 12 factors (e.g., WH, SS, EC, TN, T, and Q). Additionally, TP showed the strongest influence on the total ($R = 0.367$) and rare ($R = 0.355$) taxa, while Q ($R = 0.356$) was the highest ranked in abundant subcommunity. Similar results were observed in autumn, where abundant subcommunity and total community were affected by the same eight factors and TN had the strongest influence, while 13 factors influenced rare subcommunity, with Q as the main factor.

The distance-decay relationship is a fundamental pattern in ecology. There were significant relationships ($p < 0.001$) between Bray-Curtis distance of the bacterial community (including total taxa, AT and RT) and rkm in both seasons (Fig. 4), indicating the dissimilarity in community increased with the distance along the river. Furthermore, RT exhibited higher β -diversity than total taxa and AT. Total taxa (slope: spring = 0.142, autumn = 0.103) and AT (slope: spring = 0.156, autumn = 0.115) had higher slopes for the linear correlations than RT (slope: spring = 0.014, autumn = 0.011). The significance test showed that the slopes of total taxa and AT were statistically distinguishable from RT (spring: $p < 0.001$, autumn: $p < 0.001$), and no significant difference (spring: $p = 0.762$, autumn: $p = 0.699$) was observed between total taxa and AT. Significant distance-decay patterns (Figs. S9 and S10) were observed based on Sørensen and unweighted UniFrac distance, which further confirmed that the microbes were spatially predictable in the Yangtze River. However, the slopes of total taxa were significantly less than those of AT for unweighted UniFrac distance, which varied from the results based on the Bray-Curtis

distance. For weighted UniFrac distance, no significant distance-decay pattern was observed in RT (Fig. S11).

The VPA based on Bray-Curtis-based RDA was used to quantify the relative amount of observed variance in community composition explained by environmental and spatial factors. The results showed that these factors, selected by the forward selection procedure, explained approximately half of the community variation for the total taxa (48.7%) and AT (44.6%), which are significantly ($p = 0.001$, bootstrapping test) higher than RT (5.5%) (Table S10). For the explained portion, the pure environmental variables accounted for the main proportion ($> 78.2\%$) for all three communities, especially for total taxa (86.6%) and AT (84.6%), while the pure spatial processes and their shared effect explained small proportion ($< 21.8\%$) of community variation. The VPA performed separately for spring and autumn revealed similar results that the explained proportion in RT (5.1%–6.9%) was lower than that in total taxa (50.2%–59.3%) and AT (50.3%–58.7%), and the pure environmental variables accounted for the main explained portion. The unweighted UniFrac distance was also used for VPA, which showed similar results to the VPA-based Bray-Curtis distance (Table S11). The proportion in unexplained variation of bacterial communities indicated the potential importance of the unmeasured environmental factors, species interactions and/or stochastic processes (homogenizing dispersal and drift) for community assembly.

3.5 Quantifying assembly processes of bacterioplanktonic communities

The deviations of phylogenetic and taxonomic turnovers from null expectations were used for assessing community

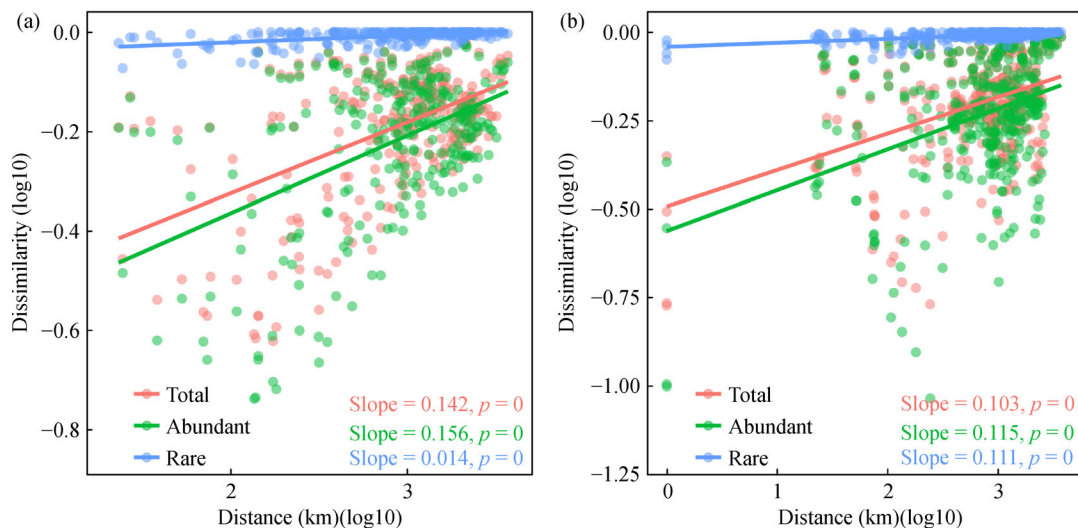


Fig. 4 Distance-decay patterns based on the Bray-Curtis distance of bacterioplankton community composition and river kilometer (rkm) in spring (a) and autumn (b), respectively. The permutational test (999 times) was used for examining the statistical significance of the distance-decay slope.

assembly mechanisms in the Yangtze River. The results of ENM revealed that stochastic assembly was the dominant assembly process in total taxa, AT and RT for both seasons, and had the highest relative contributions for AT (Fig. 5). Dispersal limitation was the main contributor of stochastic assembly for AT (84.9%–85.9%), while the undominated process was the dominant stochastic assembly for RT (51.9%–62.0%). Higher variable selection occurred in RT than in AT for both the seasons. For total taxa, 44.9%–45.2% of turnover in community composition mainly resulted from dispersal limitation, followed by undominated process (26.4%–34.4%), homogeneous selection (17.2%–21.7%), variable selection (2.4%–6.5%) and homogenizing dispersal (0.4%–0.5%), suggesting that both dispersal limitation and undominated process contributed to the stochastic assembly of total taxa. Additionally, iCAMP was applied to quantify the relative contributions of the different assembly processes. Similar results were observed, and stochastic assembly was the dominant assembly process in total taxa (59.2%–86.0%), AT (90.8%–95.6%) and RT (90.1%–90.5%), and dispersal limitation was the dominant assembly process in the AT, while the undominated process primarily governed RT. However, a higher fraction of undominated process than dispersal limitation was observed in total taxa, which differed from the results of ENM.

Mantel tests and partial Mantel tests between environmental factors and β NTI were performed to assess the influence of these factors on the stochastic and deterministic processes. The results revealed that the best predictors of β NTI differed in AT and RT. Variations in Q and SS remarkably correlated with β NTI of RT in both seasons, while pH was the only factor that had significant correlation with β NTI of AT, occurring only in autumn (Tables 1 and S12). The higher differences of Q and SS resulted in higher betaNTI (> 2) of RT in both seasons, signifying a shift of rare subcommunity assembly processes from stochasticity to variable selection.

4 Discussion

Numerous microbial surveys based on 16S rRNA gene sequencing have revealed the diversity, biogeography, and assembly process of riverine microbial communities (Read et al., 2015; Savio et al., 2015; Payne et al., 2017). Our previous study presented the integrated biogeography and assembly process of the bacterial community in the Yangtze River (Liu et al., 2018). In this study, we further revealed distinct spatiotemporal dynamics and assembly mechanisms between abundant and rare microbial subcommunities, which have not been elucidated in such large rivers previously.

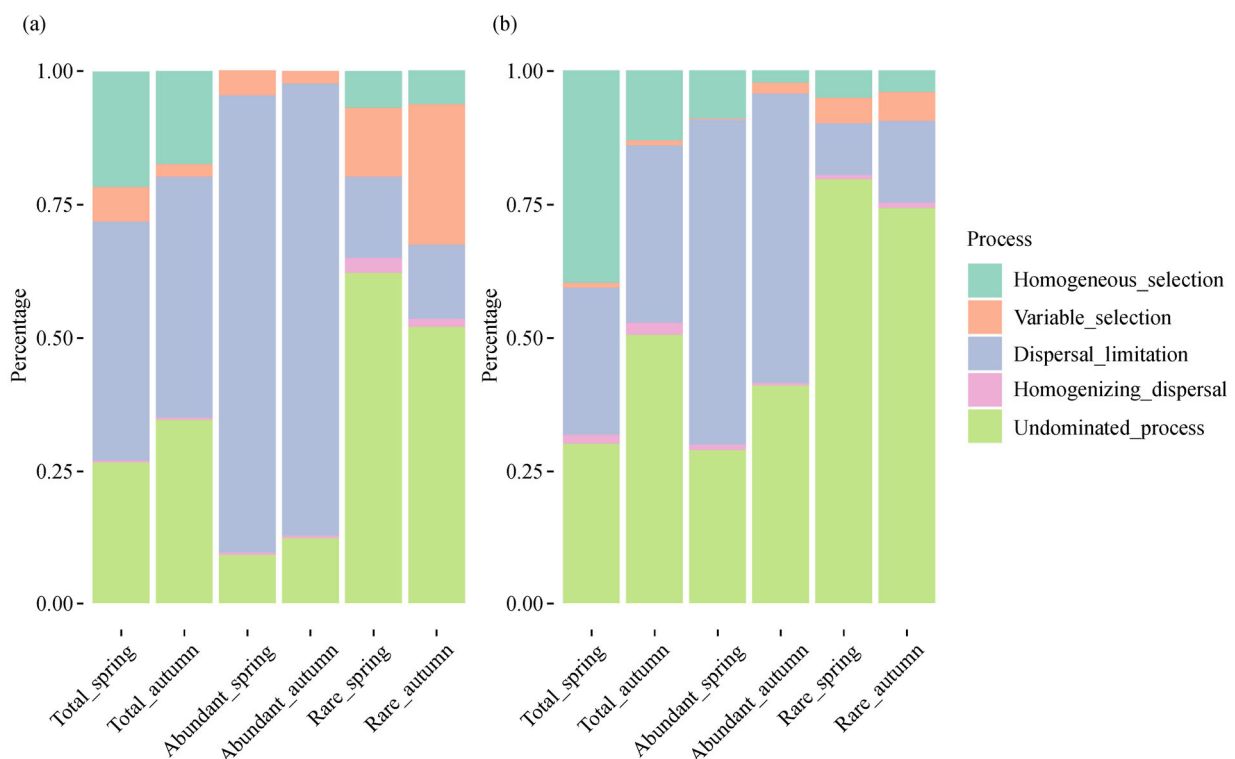


Fig. 5 The percent of turnover in community composition governed primarily by variable selection, homogeneous selection, dispersal limitation, homogenizing dispersal and undominated process for total community using the entire-community null model (a) and phylogenetic bin-based null model (b). Deterministic processes = homogeneous selection + variable selection; Stochastic processes = homogenizing dispersal + dispersal limitation + undominated process.

Table 1 Mantel analysis of the β NTI of abundant and rare taxa against environmental factors for spring and autumn. Asterisks denote significance (*, $p < 0.05$; **, $p < 0.01$)

Environmental factors	Abundant (Mantel's r)		Rare (Mantel's r)	
	Spring	Autumn	Spring	Autumn
SO ₄ ²⁻	-0.186	-0.028	-0.066	0.252*
WH	-0.101	-0.039	0.056	0.101
F ⁻	-0.090	-0.037	0.014	0.026
SS	-0.141	0.097	0.209*	0.200*
Q	-0.041	0.004	0.234**	0.433**
T	-0.069	-0.011	0.300**	0.171
pH	-0.130	0.155*	0.016	0.106
EC	0.129	-0.014	-0.009	0.363**
Cl ⁻	-0.052	0.112	-0.113	0.096
NH ₄ ⁺	0.034	-0.109	0.156	0.310**
NO ₃ ⁻	-0.039	0.065	0.132	0.049
COD	-0.077	0.052	-0.151	0.162
DO	0.077	0.103	0.018	0.045
BOD	0.022	0.054	0.075	0.299**
TP	-0.083	0.004	-0.068	0.034
TN	0.028	0.078	0.134	0.042
DOC	0.063	0.067	-0.042	0.102

Notes: a) These abbreviations of environmental factors are the same as those in Methods and Fig. S1.

4.1 Biogeography of the total bacterial communities in the Yangtze River

The differences in alpha-diversity indices between both seasons exhibited various patterns. For taxonomic diversity, the communities in autumn had higher richness and Chao indices than those in spring, indicating that a higher number of species existed in autumn. Our results were consistent with a recent microeukaryotic study in the Tingjiang River (China), where the community richness was higher in wet than dry season (Chen et al., 2019). A higher PD was observed within the autumn communities compared to their spring counterparts. PD depends on the richness of the sample (the number of ASVs), which varies from spring to autumn. After PD being standardized to the number of ASVs, there were no significant differences, which revealed that the seasonal distinction of PD was mainly caused by richness (Fig. S2).

The PCoA (Fig. 2) showed that these samples formed two clusters that exactly corresponded to the seasons, indicating that distinct bacterial community compositions existed in spring and autumn. Chen et al. (2019) observed a similar seasonal partitioning of microeukaryotic plankton in a river. This might result from the variation in hydrographic and physiochemical conditions between spring and autumn, as more than two-thirds of environmental factors significantly differed between both seasons.

Spatial variation of the bacterial community compositions showed that the landform mainly controlled their distributions at the regional scale (Fig. 3), which was similar to our previous study (Liu et al., 2018). In conclusion, the spatiotemporal dynamics of the bacterial community demonstrated niche partitioning in the Yangtze River.

4.2 Significant spatiotemporal dynamics between abundant and rare taxa

The “rare biosphere”, consisting a high number of low-abundance species, play a key role in regulating the ecological functions in river ecosystems (Pedrós-Alió, 2012; Lynch and Neufeld, 2015; Jia et al., 2018). Therefore, distinguishing the biogeography of the microbial community between AT and RT is important in understanding microbially driven ecosystem processes and functions. The PCoA and ANOSIM tests revealed that the season and landform had significant influences on AT and RT, indicating that both AT and RT exhibited significant spatiotemporal separation. Clear spatiotemporal variations for both AT and RT were observed in the previous studies on microeukaryotic and bacterial communities in a subtropical river and coastal Antarctic lakes, respectively (Logares et al., 2013; Chen et al., 2019). However, these results are inconsistent with studies on picoeukaryotic communities in the ocean (Wu et al., 2017) and bacterial communities in an activated sludge bioreactor (Kim et al., 2013), that AT exhibited significant spatiotemporal separation, but RT did not. In addition, ANOSIM tests between the two seasons showed that RT ($R = 0.551$) had a stronger statistical difference than AT ($R = 0.317$), implying that RT was more sensitive to variations in environmental factors than AT. The significantly different richness of RT between both seasons and no significant seasonal variation of AT (Fig. S3(a)) also confirmed that RT had higher environmental sensitivity than AT. We also noticed that the R value of ANOSIM tests between the two seasons for total taxa was 0.388, which was closer to R value of AT. The results of Mantel test between total community composition and abundant and rare subcommunity composition revealed that total taxa had stronger positive correlation with AT than RT for all unweighted and weighted metrics. It suggested that the degree of the seasonal difference for total taxa was more similar to AT than RT.

4.3 Influence of environmental and spatial factors on the communities

Our results showed that all communities (total taxa, AT, and RT) were significantly influenced by several environmental variables. However, the number of significant environmental factors varied across different communities, with RT being the highest in both seasons, followed by total taxa and AT, both of which were influenced by the

same environmental factors. This was in accordance with the PCoA and ANOSIM analyses, where both AT and RT exhibited clear spatiotemporal patterns, with greater variation observed in RT. In addition, the results of ENM and iCAMP also showed that higher proportions of variable selection occurred in RT than in AT for both the seasons.

The distance-decay patterns showed that total taxa, AT, and RT had spatially structured distributions in both seasons. This observation indicated that they were controlled by limited dispersal and/or spatially structured niche-related factors. Previous studies have also shown the spatial scale dependence of bacterial β -diversity, and a significant distance-decay pattern of microbial communities was observed at local scales rather than at regional scales in various habitat types (Martiny et al., 2011). For example, the spatial turnover of activated sludge bacterial communities is scale-dependent, and no significant distance-decay pattern has been observed at intercontinental scales (Wu et al., 2019). Astorga et al. (2012) observed that diatom communities were only significantly related to geographic distance at small spatial extents in rivers. However, we observed significant distance-decay patterns at regional scales in total taxa, AT, and RT for both seasons, suggesting the important role of dispersal limitation of bacterial species in large rivers. Gao et al. (2019) exhibited significant distance-decay patterns of diazotrophic and bacterial communities at regional scales, and the slopes of the distance-decay curve were dependent on spatial scales in paddy soil. The distance-decay slopes of AT were significantly ($p = 0.001$) steeper (approximately 10 times) than RT's distance-decay slopes for different dissimilarity metrics, suggesting that the spatial turnover rates of AT were higher than those of RT. No significant difference of slopes between total taxa and AT in both seasons, suggesting that they had similar spatial turnover rates. They could result from not only dispersal limitation, but also spatially structured environmental factors.

Although numerous environmental factors had a significant effect on RT, the VPA results showed a small fraction of community variation explained by geographic distance and environmental variables, indicating that these factors played a minor role in governing rare subcommunities. Several previous studies also showed small fraction of rare subcommunity variation explained by geographic distance and environmental variables in different habitats (Mo et al., 2018; Zhang et al., 2018). Half of the community variation in total taxa and AT was explained by environmental and spatial factors, indicating stronger influences of these factors in controlling AT than RT. Although VPA has been widely used to infer the influences of ecological processes, one should cautiously approach partitioning community variation by VPA, which has been reported as an inefficient method to assess the relative importance of different variables in shaping microbial community structure (Gilbert and Bennett, 2010; Smith

and Lundholm, 2010). This inefficiency may be caused by ignoring certain unmeasured environmental factors, which can be highly related to community variation (Lindström and Langenheder, 2012; Stegen et al., 2013). Another reason is that co-occurrence correlations among microorganisms may cause biases when VPA is applied to quantify community assembly (Lima-Mendez et al., 2015; Wei et al., 2016). In addition, the co-variation of geospatial and environmental factors also cloud caused the imprecise results (Zhang et al., 2018). Hence, we further used null model to quantify the relative importance of each assembly process in this study.

4.4 Distinct assembly mechanisms of abundant and rare taxa

Revealing the fundamental mechanisms of the assembly process is a central issue in microbial ecology (Nemergut et al., 2013). Although both selective and neutral processes have been assumed to jointly affect community assembly in various ecosystems (Stegen et al., 2012; Wang et al., 2013; Evans et al., 2017), further studies are necessary to quantify the relative influences of these processes on community assembly. Here, we employed the null model (ENM and iCAMP), which did not require relating community compositions to environmental factors, to quantify the relative contributions of each assembly process driving the biogeography in the Yangtze River. The results of both ENM and iCAMP revealed that stochastic assembly was critical for AT and RT. Several studies (Table S13) showed similar results for bacteria in Tibetan Plateau (China) grassland soils (Ji et al., 2020), and picoeukaryotes in subsurface layer of marginal seas in the north-western Pacific Ocean (Wu et al., 2017), this differs from previous studies reporting that rare subcommunities were mainly limited by deterministic process for fungi in agricultural fields of eastern China (Jiao and Lu, 2020a), bacteria in eutrophic Lake Nanhu (Wuhan, China) (Wan et al., 2021a), and bacteria in salinized agricultural soils (Wan et al., 2021b) (Table S13). The contrasting phenomenon might be attributed to differences in geography and habitats (Shi et al., 2018). Moreover, stochastic processes were further divided into homogeneous dispersal, dispersal limitation, and undominated process. We observed that dispersal limitation primarily governed AT, whereas undominated process was crucial in controlling rare subcommunity assembly with a stochastic balance between the gain and loss of microorganisms (e.g. stochastic births, deaths, and immigration). The greater influence of dispersal limitation on AT than RT was supported by the significant distance decay pattern of AT with steeper slopes. In addition, VPA showed that AT was strongly correlated with variations in environmental factors (approximately half of the variance explained), as compared to the rare assemblage. However, the results of the null models did not display a higher proportion of

variable selection in the AT. Ji et al. (2020) also showed similar results for abundant bacterial subcommunity in Tibetan Plateau (China) grassland soils. Besides possible limitations of statistical approaches, the co-variation of geospatial and environmental factors might bring bias. Overall, the results of distance decay patterns and the null model supported the notion that dispersal limitation and undominated process dominate the assembly of AT and RT in the Yangtze River, respectively.

We also explored the community assembly of the total taxa. Although the research spatial scale in this study was at a regional scale (4300 km) with several changing environmental factors, we still observed that total community assemblies were mainly shaped by stochastic processes, which was consistent with AT and RT. Chen et al. (2019) also revealed that these riverine microeukaryotic communities were strongly driven by stochastic process at a small scale (< 100 km). However, several prior studies have reported that deterministic assembly governed the planktonic bacterial communities within multiple lakes (Jiao et al., 2020), and overall community assembly was primarily governed by homogeneous selection in agricultural fields (Jiao and Lu, 2020b). For total taxa, the proportions of dispersal limitation were higher than the undominated process in both seasons, which was same as AT. This was similar to the results of PCoA and ANOSIM that the effects of season on total taxa were more similar to AT than RT. In addition, higher effects of homogeneous selection on total taxa than those on AT and RT was revealed in both seasons, which indicated a phylogenetically close cluster than the expectation of the null model. Horner-Devine and Bohannan (2006) demonstrated that the phylogenetic clustering of bacterial communities could result from environmental filtering.

In addition, we found that the β NTI of RT was strongly correlated with Q and SS in both seasons, indicating that Q and SS might play a crucial role in balancing the deterministic and stochastic processes for RT. A high Q value meant high fluidity of water, which promoted the dispersal of bacterioplankton, especially suppressing the dispersal limitation of RT. Suspended particles are of primary importance in the transport and transformation of substances, providing microorganisms to different habitats (Savio et al., 2015). A higher SS could transfer more diverse bacteria in the river ecosystem. Therefore, Q and SS mediated the balance between the deterministic and stochastic processes of RT in the Yangtze River.

5 Conclusions

This study provided the biogeographic profiles of abundant and rare bacteria along the 4300 km continuum of the Yangtze River. Our results revealed a significant spatiotemporal variation for RT and AT, and ANOSIM further indicated that RT had a distinct separation as compared to

AT, suggesting stronger spatiotemporal stress on RT than AT. Although RT was significantly influenced by additional environmental factors as compared to AT, environmental and spatial factors jointly explained less spatiotemporal shifts in RT than AT, indicating that there were other factors playing a relatively larger role in influencing RT. Significant distance decay patterns were exhibited in AT and RT at regional scales, and the former had steeper slopes than RT in both seasons, corresponding to stronger effects of dispersal limitation on AT than RT. Although stochastic processes strongly shaped both AT and RT, AT was mainly dominated by dispersal limitation, which was consistent with the results of distance decay analysis, whereas RT was heavily influenced by undominated process, followed by variable selection and dispersal limitation. SS and Q served as good predictors of the assembly processes in RT in the Yangtze River. Total taxa had similar spatiotemporal dynamics and distance decay patterns as AT. The same environmental factors influencing total taxa and AT and dispersal limitation predominating total taxa and AT assembly similar assembly mechanisms between total taxa and AT. Our study contributes to the understanding of the biogeographical dynamics of abundant and rare bacterioplankton subcommunities and sheds light on the underlying assembly processes in the Yangtze River.

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